Cuticle Strength and the Size-Dependence of Safety Factors in *Cancer* Crab Claws

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Abstract. The surprising incidence of nonlethal skeletal fractures implies that many organisms operate near their upper performance limits, yet we know little about the loads at which biological structures break or about the material properties of those structures. In addition, biologically realistic estimates of how closely normal maximal loads approach breaking strengths (*i.e.*, safety factors) remain elusive. We measured cuticular breaking strength (a material property) and safety factors (breaking force/maximum biting force) for intact claws of six species of predatory *Cancer* crabs (Crustacea, Brachyura). Cuticular breaking stresses in *Cancer* claws (40–120 MN m^{-2}) exceeded those reported for the carapace of shore crabs (*Carcinus*) and swimming crabs (*Scylla*), but were similar to published values for the claws of stone crabs (*Menippe*). Cuticular breaking strength increased towards the tip of the pollex (fixed finger), correlated with visible changes in the claw cuticle, but decreased with increasing claw size. Safety factors of the pollex varied within and among *Cancer* species and ranged from 2 to 7. Safety factors increased with increasing claw size ($\propto$ manus length$^{0.6}$), due to proportionally thicker cuticle ($\propto$ manus length$^{1.31 \pm 0.078}$) and proportionally lower maximum biting forces ($\propto$ manus length$^{1.49 \pm 0.082}$). Why larger crabs have proportionally lower biting forces remains an important unsolved problem. The higher safety factors of larger claws appear adaptive, however, since costs of failure and unpredictability of cuticle strength increase with increasing size. Patterns of intraspecific size-dependence offer an attractive test of whether safety factors vary adaptively. A brief review of the literature suggests that positive size-dependence often signals adaptive variation in safety factors, whereas negative size-dependence may signal the action of constraints on growth or form.

Introduction

Rather unexpectedly, structures as diverse as mollusc shells (Vermeij, 1982; Brandwood, 1985), crab claws (Juanes and Hartwick, 1990; Taylor *et al.*, in press), the teeth of living and extinct carnivorous mammals (Van Valkenburgh, 1988; Van Valkenburgh and Hertel, 1993), the antlers of ungulates (Kitchener, 1991), and the limbs of birds and mammals (Buikstra, 1975; Currey, 1984; Brandwood *et al.*, 1986) exhibit high rates of nonlethal failure in natural populations. The skeletons of many organisms therefore appear to operate near their upper performance limits under normal living conditions, and safety factors (*e.g.*, the ratio of breaking strength to maximum load) should be under constant pressure to evolve. Yet enhanced durability bears a price and, like most attributes of organisms, must reflect a balance between the benefits of increased performance and the costs of construction, maintenance, and possible failure (Alexander, 1982).

Because explicit predictions exist for how safety factors should vary under different situations (Alexander, 1981, 1997), tests may be conducted to assess how closely biological structures approach theoretical design optima. Compared to analyses of among-species differences, those of size-dependent variation within species offer even more rigorous tests because fewer potentially confounding factors vary and predictions are therefore more precise (Currey, 1977; Niklas, 1994). For example, for the brachyuran crabs we studied, larger crabs should exhibit higher claw safety factors for several reasons: (a) stress cracks and wear have more time to accumulate between molts, which increases the unpredictability of claw strength in larger crabs, (b) the negative ecological impact of lost or damaged claws (Juanes

and Smith, 1995) will be more prolonged or severe for larger crabs, and (c) larger crabs may experience a greater range of extreme forces because claws are used increasingly for aggression (Juanes and Smith, 1995).

Intraspecific size-dependence of safety factors may also reveal unexpected geometrical or ontogenetic constraints that preclude an optimal design. For example, if cuticle thickness varies in proportion to body mass within a species, the critical buckling loads of walking legs in smaller insects must greatly exceed the likely maximal loads experienced to ensure an appropriate critical buckling load at larger body size (Prang, 1977). Similarly, the stems of small horsetails, *Equisetum,* are mechanically "overbuilt" by roughly 10 times compared to larger plants (Niklas, 1989). In both of these examples of narrow, tubular support systems, mechanical and growth considerations appear to conflict.

Unfortunately, biologically realistic distributions of strength and, particularly, load are difficult to measure with confidence for most structures, so estimates of safety factors of individual organisms are often indirect. Typically, safety factors are estimated either (a) by computing or measuring maximal loads on aggregate samples and then comparing these to standard estimates of material properties or theoretical estimates of failure strengths (Alexander, 1981; Biewener, 1990; Niklas, 1994; Biewener and Dial, 1995; Claussen and Maycock, 1995), or (b) by computing an average maximum load and an average breaking force measured on different samples of individuals (Lowell, 1985, 1987; Friedland and Denny, 1995). Crab claws offer a particularly attractive opportunity for direct study of the intraspecific size-dependence of safety factors because both maximal closing forces and breaking forces can be measured on an individual claw. In addition, because the entire cuticle is assembled anew following a molt, the intermolt interval may be considered a "lifetime" for a claw (Taylor *et al.,* in press) in the same way as ungulate antlers that are also renewed annually (Kitchener, 1991). Therefore, we could examine intraspecific variation that would otherwise not be apparent using indirect approaches.

We examined the size-dependence of safety factors in the claws of six closely related species of *Cancer* crabs, to test whether safety factors varied in a manner more consistent with adaptation or constraint: do claw safety factors increase with increasing crab size—as would be expected because of increased unpredictability of cuticle strength, increased costs of failure, and possibly increased unpredictability of load distribution (Juanes and Smith, 1995)—or do they decrease with increasing crab size, because geometric or ontogenetic constraints associated with the growth of "external" tubular support systems yield structures that must be disproportionately strong at smaller sizes to retain function at larger sizes, as suggested for insect legs (Prang, 1977) and the shoots of horsetails (Niklas, 1989).

Throughout the paper, we apply the verb *to bite* to the action of claws. Although most commonly used in reference to mouthparts, we invoke it here because anyone attacked by a large crab would surely exclaim that they had been bitten rather than squeezed, grasped, pinched, or nipped, and because in carnivorous brachyuran crabs claws function to crush prey, or to tear apart the flesh, much like vertebrate jaws.

Materials and Methods

Experimental animals

Crabs collected from various shallow-water sites near Bamfield, British Columbia, Canada (see Table I for size ranges) were held in running seawater aquaria and fed shucked mussels daily (*Mytilus* spp.). Biting forces of claws were measured within 7 days of collection, as maximum force and consistency declined with time in the laboratory (G. M. Taylor, unpubl. obs.). Crabs with damaged or regenerating claws were not used, nor were crabs suspected to be early or late intermolt (Taylor *et al.,* unpubl. obs.) because biting forces (Kaiser *et al.,* 1990) and cuticle properties (Horst and Freeman, 1993) may vary substantially over the intermolt interval.

To minimize among-investigator variation, GMT mea-

Table I

Crab size, load position, and number of bites obtained per claw for six species of Cancer *crabs*

Species	n_t	Carapace width (mm) Mean (SE, min., max.)	n_c	Load position (SE)*	Mean # bites per claw (SE)
C. antennarius	14	76.1 (3.20, 56.4, 99.1)	28	0.89 (0.005)	7.8 (0.07)
C. branneri	8	51.0 (1.30, 44.9, 55.5)	16	0.92 (0.003)	6.9 (0.48)
C. gracilis	9	91.4 (3.13, 74.9, 103.8)	18	0.94 (0.002)	7.1 (0.75)
C. magister		122.6 (2.58, 111.4, 139.2)	23	0.94 (0.004)	7.8 (0.42)
C. oregonensis	15	33.1 (0.76, 29.4, 39.9)	30	0.86 (0.004)	7.4 (0.18)
C. productus	16	89.6 (6.26, 60.1, 130.1)	31	0.91 (0.006)	8.3 (0.20)

n_t = number of individual crabs, n_c = number of claws for which biting force measurements were obtained; not all claws were included in all analyses (see Methods).

* Position at which biting force or breaking strength was measured, expressed as a proportion of the pollex length (line d–e, Fig. 1).

sured biting force in all cases and AB measured claw morphometrics and breaking strengths.

Biting force measurements

Crabs were encouraged to grasp a force gauge with their claw and bite as hard as possible while held firmly in the air by the proximal portions of both chelipeds so other movement would not affect the biting force measurements. The pollex (fixed finger) was inserted into a lower fixed steel ring, and the dactyl into an upper ring mounted on a flexible 2-mm-thick steel beam bearing two strain gauges (Bean BAE-13-250BB-350TE; 350Ω) that were connected to a Wheatstone bridge and a chart recorder. The rings were positioned at the same point for all claws: just inside the tip of the dactyl and pollex, distal to the first tooth (*i.e.*, the same position as the load when breaking the claw, Fig. 1, Table 1). To ensure comparable biting forces among claws of different size, the distance between the inner margins of the rings was adjusted to about 60% of the maximum gape at this position for each claw. Before and after each session of 7–10 crabs, deflections of the upper ring were calibrated with five known weights (4.6–112 N) that exceeded the full range of observed maximum biting forces. The average of these two curves was used to digitize calibrated biting forces after each session.

Biting forces were measured for both claws of each crab in succession. To avoid possible biases, the first measurement alternated between the right and left claw on successive trials. At most, two measurements were obtained per claw per day, separated by at least 4 h. Mean number of trials per claw varied from 6.9–8.3 among species (Table 1); claws with fewer than four trials were excluded from the analyses. Though median-maximum biting force exhibited less statistical noise, the allometric coefficient was statistically indistinguishable from that for extreme-maximum biting force (see Table Ve *versus* Vf), so extreme-maximum biting forces were used to permit comparison with previously published values.

Morphometry and breaking force

Claw and cuticle dimensions (Fig. 1) were digitized with a Summagraphics drawing tablet (20 dots/mm resolution) from enlarged (8–12×), calibrated camera lucida drawings of autotomized claws (Wild M5A dissecting microscope with a 0.3× reducing lens, if necessary). This method is accurate to within ±1% (Smith and Palmer, 1994).

Claws were broken within 1 h of autotomy and held in seawater or kept wet continuously until broken. Breaking forces were typically measured within 2–3 days of the last biting force, and never more 14 days after the last biting force. To obtain breaking forces, claws were clamped rigidly, and a container was suspended from the tip of the pollex by a loop of 4 mm diam. steel wire (Fig. 1). Lead
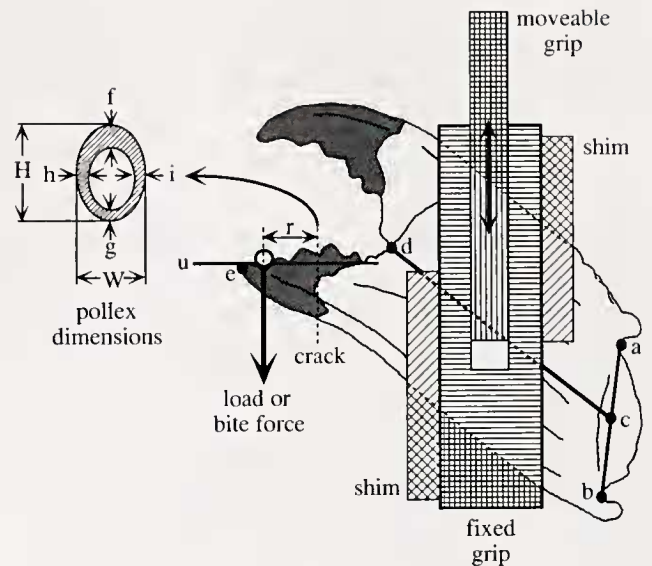

Figure 1. Clamping orientation and dimensions of a *Cancer* claw. (a) and (b) are the dorsal and ventral hinge points of the manus, and (c) is the midpoint between them. *Manus length*: line-segment (c)–(d) (*i.e.*, chela length excluding the pollex). *Pollex* (= *fixed finger*) *length*: line-segment (d)–(e). *Moment of the load at failure*: the double-headed arrow labeled r. Moveable (vertical shading) and fixed (horizontal shading) pieces of acrylic plastic (Plexiglas) gripped the claw at about the midpoint of the manus, and softer wooden shims (angled-shading) reduced the risk of twisting and unwanted damage to claws under load; cross-hatching indicates the acrylic or shim was solid at that point. These acrylic pieces and shims had notches cut in them to fit either the right or left claw as snugly as possible (not visible in the figure as they were parallel to the plane of view). Claws were aligned so the load was oriented perpendicular to the *gum line* (= occlusal surface) of the pollex (line u; a best-fit line through the bases of the teeth). The load was applied just inside the tip of the pollex (open circle). Pollex height (*H*) and width (*W*), as well as cuticle thickness at the dorsal (*f*), ventral (*g*), medial (*h*) and lateral (*i*) margins, was measured at the point of fracture (*crack*) in a plane parallel to the load vector and perpendicular to the long axis of the pollex.

weights to about 80% of the estimated breaking force were gently added, and then sand was poured into the container at a constant rate (approx. 5 g/s) until the claw broke. The container and contents were then weighed to the nearest gram.

After the claw failed, the location of the load wire and the fracture margin were recorded on each claw drawing. Cuticle thickness at the point of failure was measured by orienting the fracture surface of the broken pollex towards the viewer so that the line of sight was parallel to the occlusal surface of the pollex (line u, Fig. 1). Pollex width (*W*), as well as cuticle thickness at the dorsal (*f*), ventral (*g*), medial (*h*) and lateral (*i*) margins, was digitized from enlarged drawings of this orientation. In addition, the height of the pollex immediately below the point of crack initiation and perpendicular to the occlusal surface was also digitized (*H*, along the vertical dashed line labeled *crack*, Fig. 1). The actual fracture plane was not always perpendicular to the

occlusal surface, so stresses were calculated twice, once using all the data and once using only breaks that were within $\pm 30°$ of the vertical dashed line labeled *crack* (Fig. 1).

Analyses

Regression analyses and analyses of variance were conducted with StatViewII (ver. 1.03, Abacus Concepts). Tests for differences in slopes between sexes and among species, and common slopes, were computed by means of analysis of covariance (ANCOVA; SuperANOVA ver. 1.11, Abacus Concepts).

Ultimate stress (σ_b, MN m^{-2}) of the cuticle surface at the point of fracture—*extreme fiber stress* in the engineering literature—was estimated using the linearly elastic theory (Biewener, 1982)

$$\sigma_b = F_b r c I^{-1} \qquad \text{(Equation 1)}$$

where

F_b = breaking force (in newtons, N).

r = moment arm (center of the load wire to the point of crack initiation, in mm; Fig. 1).

c = distance from the neutral axis of the pollex to the upper surface ($H/2$, where H = height of the pollex parallel to the load vector immediately below the point of crack initiation, in mm; Fig. 1). Ideally, c should be computed from the centroid (the presumed neutral axis) of the pollex cuticle in a plane perpendicular to the occlusal surface at the point of crack initiation, but we did not have sufficiently detailed measurements of the distribution of cuticle to do this, so we assumed that the neutral axis was at the midpoint of the cross-section of the pollex (H, Fig. 1).

I = second moment of area (mm^4) computed parallel to the load vector immediately below the point of crack initiation as $I = (I_u + I_l)/2$, where $I_u = (\pi/64)\{(WH^3) - [(W - h - i)(H - 2f)^3]\}$ and $I_l = (\pi/64)\{(WH^3) - [(W - h - i)(H - h - i)^3]\}$ (see Fig. 1 for cuticle dimensions and Alexander (1983) for the formula). I was computed separately for the upper (I_u) and lower (I_l) half of the cross section of the pollex because the upper cuticle margin was roughly twice as thick as that of the sides or bottom. Side thicknesses (h and i of Fig. 1) instead of measured bottom thickness (g) were used to compute I_l because bottom thickness varied with fracture angle, and because in claws where the bottom thickness could be measured reliably, it did not differ from the side thickness (data not shown).

Ultimate stress (σ_b) could not be computed for all claws for which we obtained safety factors because a few claws broke at the base of the pollex adjacent to the opening where the dactyl inserted, so dimension (f) could not be measured.

Breaking force variability of different sized crabs was assessed by (a) computing residuals from a least-squares linear regression of untransformed breaking force (Y) on untransformed manus length (X) for each species separately (sexes were pooled), (b) dividing the sample for each species into two roughly equal-sized groups (smaller and larger) based on carapace width, and (c) conducting a Levene's test on the absolute values of the residuals (2-way ANOVA: species $\times$ size group). This analysis was also repeated using log-transformed variables.

Least-squares linear regressions were used to obtain coefficients of allometry throughout the analyses, even though such coefficients may be underestimated as the goodness-of-fit to a line declines (LaBarbera, 1989). They were nonetheless preferred over alternative Model II regressions in our study for two reasons. First, the uncontrolled variation in the dependent variable was substantially greater than that in the independent variable (*e.g.*, see Tables II and IV), so a Model I analysis was more appropriate. Second, we wished to compare both slopes and intercepts among species by ANCOVA (*e.g.*, Tables III and V below), and the validity of P values from such comparisons based on Model II regressions is open to question.

The statistical significance of differences between pairs of model coefficients was computed using two-sample t tests for unequal sample sizes (Sokal and Rohlf, 1995).

Results

Breaking force and breaking-force variability

Although claws broke at many different locations along the pollex, most breaks fell either towards the base (0.2–0.4 of standardized pollex length), near the proximal margin of the tanned cuticle (the black ends to the fingers of many brachyuran crab claws), or towards the tip (0.6–0.8 of standardized pollex length, Fig. 2a). Nonetheless, even though pollex diameter varied substantially from the base to the tip, the location of the break had no effect on the force at which the pollex broke after controlling statistically for the effects of claw size (Fig. 2a). Only 5 claws out of 141 shattered along the lower margin of the pollex, as would occur when failure was due to local buckling (Wainwright *et al.*, 1976), and these were excluded from the analyses.

The fracture plane, however, was not always perpendicular to the upper pollex surface (*i.e.*, parallel to the load vector). Most commonly, cracks deflected proximally towards the pollex base. In some cases, the fracture plane deviated by more than 30° from the load vector. Such cracks tended to be concentrated towards the tip of the pollex and yielded somewhat more variable estimates of breaking strength (Fig. 2b).

Larger crabs exhibited significantly more variable break-

Table II

Size-dependence of pollex cuticle-strength for claws from six species of Cancer *crabs*

Species	n	Slope (SE)	Intercept (SE)	P	r
a) log(ultimate stress, MN m^{-2}) (Y) *vs.* standardized pollex position (X) (see Fig. 2b for data)					
1. *C. antennarius*	28	0.178 (0.0953)	1.715 (0.0200)	0.073	0.344
2. *C. branneri*	12	0.427 (0.1537)	1.817 (0.0325)	0.019	0.660
3. *C. gracilis*	12	0.195 (0.1100)	1.684 (0.0285)	0.106	0.490
4. *C. magister*	17	0.262 (0.2060)	1.630 (0.0563)	0.223	0.312
5. *C. oregonensis*	28	0.198 (0.1334)	1.712 (0.0256)	0.151	0.279
6. *C. productus*	28	0.618 (0.1363)	1.377 (0.0250)	<0.001	0.664
7. All pooled	125	0.213 (0.0582)	1.702 (0.0136)	<0.001	0.313
8. All pooled*	60	0.178 (0.0971)	1.716 (0.0171)	0.073	0.234
9. All pooled†	125	0.162 (0.0478)	−0.095 (0.0112)	0.001	0.292
b) log(ultimate stress, MN m^{-2}) (Y) *vs.* log(manus length, mm) (X) (see Fig. 3 for data)					
1. *C. antennarius*	28	−0.615 (0.2023)	2.642 (0.0183)	0.005	0.512
2. *C. branneri*	12	−1.123 (0.8404)	3.352 (0.0399)	0.211	0.389
3. *C. gracilis*	12	−0.433 (0.4542)	2.408 (0.0313)	0.363	0.289
4. *C. magister*	17	−1.146 (1.3504)	3.562 (0.0578)	0.409	0.214
5. *C. oregonensis*	28	−0.575 (0.7015)	2.448 (0.0263)	0.420	0.159
6. *C. productus*	28	−0.811 (0.1776)	2.926 (0.0250)	<0.001	0.667
7. All combined‡	125	−0.751 (0.1447)	2.842 (0.2042)	<0.001	0.573
8. All combined‡,§	125	−0.624 (0.1352)	0.820 (0.1908)	<0.001	0.591

Least-squares linear regression equations. n = number of individual crabs; SE = standard error; r = correlation coefficient.

* Excluding claws that broke at more than 30° from the load vector (Fig. 2b).

† Based on residuals from separate regressions of log(ultimate stress) *versus* log(manus length) for each species.

‡ Common slope from a one-factor ANCOVA with species as the grouping variable.

§ ANCOVA recomputed using residuals from a single regression of log(ultimate stress) *versus* standardized pollex position for all species combined.

ing forces ($P = 0.036$, Levene's test), but this difference was not significant when computed for log-transformed size and biting force ($P = 0.67$). Therefore in absolute terms, breaking forces were more variable for larger claws, but the variability appeared to be proportional to claw size.

Under natural conditions, claws may fail mechanically in ways other than the breakage of the pollex that we examined in this study. For example, claws might fail because the dactyl tip breaks, rather than the tip of the pollex, or because the dactyl condyles become disarticulated from their sockets. Among the 81 injured claws we observed in field-collected crabs, the dactyl tip was broken more frequently than the pollex tip (46 *versus* 33), however none exhibited a dislocated dactyl. Disarticulated dactyls are occasionally observed in field-collected crabs (G. M. Taylor, unpubl. obs.), but this mode of failure appears quite rare. Therefore we believe our study has focused on the most biologically relevant form of claw failure: fracture of one of the fingers.

Cuticle strength of claws—patterns

Although breaking force did not vary along the pollex, the ultimate stress (force per unit area, σ_b)—a measure of the ability of claw cuticular material to resist failure in tension—did (Fig. 2b). When data for all species were considered together, ultimate stress increased distally from a mean of 53 at 0.1 to a mean of 78 MN m^{-2} at 0.9 of the

standardized pollex length (Fig. 2b; $P < 0.001$, Table IIa-7). Ultimate stress (σ_b) of claws that fractured along a line deviating by more than 30° from the load vector (Fig. 2b) was somewhat more variable because of increased uncertainty about the true cuticle thicknesses below the site of crack initiation. However, exclusion of these points did not significantly alter the slope or intercept of this relationship ($P = 0.75$; compare row a-8 to row a-7 in Table II). Because ultimate stress (σ_b) declined with increasing claw size (see below), the effect of claw size might have confounded the effect of crack location. Here again, though, an analysis of the residuals, where residuals were computed separately for each species from a regression of log(ultimate stress) *versus* log(manus length), also yielded a slope that did not differ significantly from the original untransformed data ($P = 0.50$; compare row a-9 to a-7 in Table II). Slopes of this relationship appeared to vary among species (rows a1–a6, Table II); however, these differences were not significant statistically ($P = 0.2$; see Table Va). Therefore, regardless of how the analysis was conducted, the cuticle was nearly 50% stronger at the pollex tip than at the base (0.9 *versus* 0.1 of standardized pollex length, respectively).

For all six *Cancer* species, breaking or ultimate stress (σ_b) declined with increasing claw size (Fig. 3, Table IIb). This decline was significant statistically only for *C. antennarius* and *C. productus* (Table IIb-1,6) when species were
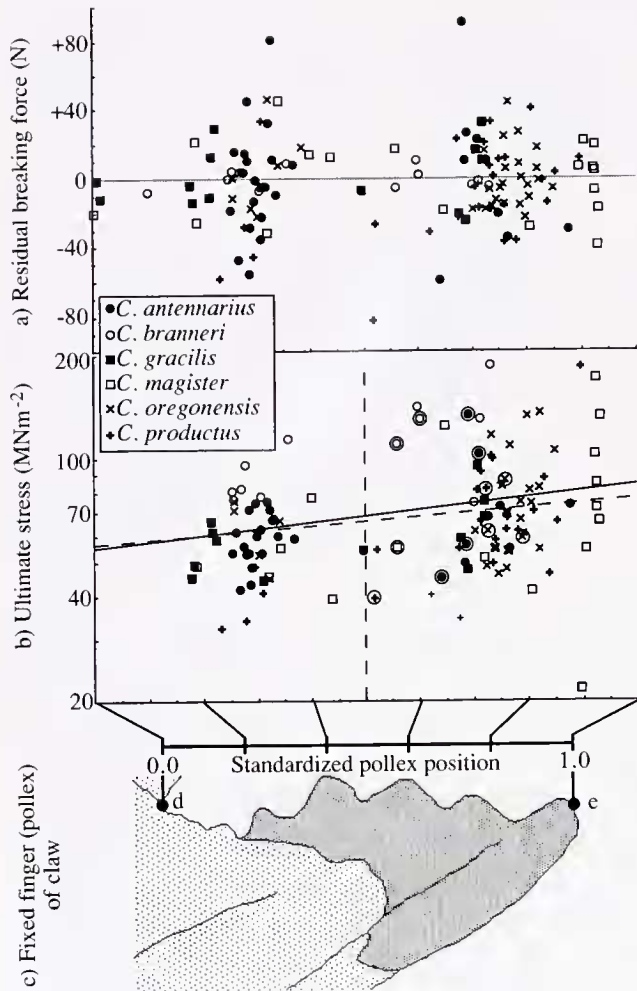
Figure 2. (a) Deviation of breaking force from that expected for a given claw size (manus length), and (b) the computed ultimate stress (σ_b; meganewtons per meter squared, MN m^{-2}) at which the cuticle failed, both as a function of standardized position along the upper margin of the pollex between the insertion point of the closer apodeme (landmark d) and the tip (landmark e) for six species of *Cancer* crabs. (c) The pollex, or fixed finger, of a *C. productus* claw illustrating how *standardized position* was determined; claws of other *Cancer* species differ in shape and number of teeth (Nations, 1975). The darker portion of the finger is often black in life, and both harder and stronger (Melnick *et al.*, 1996). Points surrounded by circles above 0.5 standardized pollex length indicate claws for which the fracture plane did *not* deviate by more than 30° from the load vector (see methods). The solid line in (b) indicates a least-squares linear regression through all the data, whereas the dashed line applies only to claws for which the fracture plane did *not* deviate by more than 30° from the load vector (see Table IIa7,8 for regression statistics).

analyzed separately because of the smaller size ranges for the other species. However, a 1-factor ANCOVA with species as the grouping variable revealed that slopes did not differ significantly among species ($P = 0.96$; see Table Vb) and that the common slope was highly significant ($P < 0.001$) (Table IIb-7). To control for possible effects of crack location (Fig. 2b), an ANCOVA was also conducted on

residuals from the regression of Table IIa-7. This too revealed no significant difference in slopes among species ($P = 0.97$; see Table Vb). The common slope from ANCOVA was also highly significant statistically ($P < 0.001$) and did not differ significantly from the slope obtained for the original untransformed data ($P = 0.52$; compare row b-8 to b-7 in Table II). Therefore, regardless of how the analysis was conducted, cuticle strength decreased by approximately 40% with a doubling of claw size (measured as manus length).

This decline was not simply an artifact of our computations for intact claws; if it were, all claws should fall upon the same regression line, and *C. oregonensis* clearly does not (Fig. 3). This decline was also not an artifact of using manus length as the arbitrary measure of claw size, because nearly identical results were obtained using total claw wet weight as the covariate (results not shown).

Finally, size-adjusted breaking or ultimate stress (σ_b) differed up to twofold among *Cancer* species ($P < 0.001$, ANCOVA; Table III). For a given claw size, *C. magister* had the strongest pollex cuticle and *C. oregonensis* the weakest. *Post-hoc* tests, however, revealed that most of the statistical support for interspecific variation arose from the unusually low value for *C. oregonensis*, although *C. magister* did differ from *C. antennarius* when standardized by manus length. Unfortunately, we cannot say with much confidence whether the significantly lower cuticle strength of *C. oregonensis* would also obtain for pristine, unworn claws because *C. oregonensis* are undoubtedly older, for a given body size, than the other *Cancer* species and their claws may simply have accumulated more fatigue or wear in the field prior to measurement.

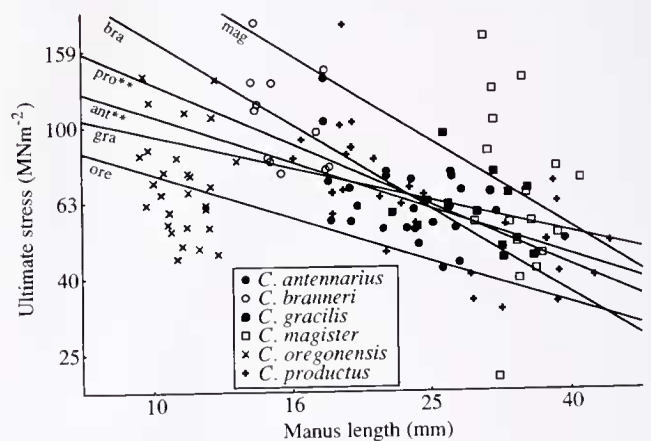Differences in our estimates of cuticle strength among

Figure 3. Cuticle ultimate stress (σ_b; meganewtons per meter squared, MN m^{-2}) as a function of claw size (manus length, mm) for six species of *Cancer* crabs. Solid lines indicate least-squares linear regressions for each species. See Table II for statistics. **$P < 0.01$. Note that both axes are on a logarithmic scale. Three-letter abbreviations adjacent to each line indicate the first three letters of each species' name.

Table III

Average, size-adjusted pollex cuticle-strength for claws from six species of Cancer *crabs*

Species	Mean (SE)* log(ultimate stress)	Detransformed mean ultimate stress (MN m^{-2})			
		By length*	Post-hoc†	By weight‡	Post-hoc†
C. magister	1.967 (0.0444)	92.7	a	80.7	a
C. branneri	1.919 (0.0434)	83.0	ab	83.6	a
C. gracilis	1.884 (0.0447)	76.6	ab	70.2	a
C. productus	1.851 (0.0281)	71.0	ab	66.1	a
C. antennarius	1.839 (0.0271)	69	b	71.7	a
C. oregonensis	1.641 (0.0474)	43.8	c	50.8	b

* Adjusted means ($\pm$ SE) from a one-factor ANCOVA (species was the grouping factor; see Table IIb-7 for regression statistics) for a common manus length of 20.9 mm. Differences among adjusted means were highly significant ($P < 0.001$).

† Results from a Tukey-Kramer post-hoc test (Sokal and Rohlf, 1995) on adjusted means (prior to detransformation); letters indicate means that were not significantly different from each other at a table-wide significance level of 0.05.

‡ Detransformed means for a standard claw wet weight of 3.6 g from a similar one-factor ANCOVA using claw weight as opposed to manus length as the covariate (regression statistics not shown).

species were potentially complicated by differences in cuticle thickness. Even though *C. oregonensis* claws have a much larger area of black cuticle at the pollex tip (G. M. Taylor, unpubl. obs.), and even though this material is probably considerably stronger than cuticle on the remainder of the claw (Melnick *et al.*, 1996; this study), *C. oregonensis* claws exhibited the lowest cuticle strength of all the *Cancer* species we examined (Table III). *C. oregonensis* also had the thickest cuticle on the occlusal surface of the pollex (1.9 mm). It was nearly 2.5 times thicker than that of *C. magister* (0.7 mm), which had the highest cuticle strength (adjusted means from ANCOVA for a standard manus length of 20.9 mm, data and analysis not shown). Because the tanned and harder cuticle at the pollex tip forms only the outermost layer of the cuticle, and an additional layer of "normal" cuticle appears to lie underneath it (G. M. Taylor, unpubl. obs.), our estimates of cuticle strength, which were based on the total thickness of the cuticle, may underestimate the actual strength of this tanned cuticle and therefore potentially confound some of the differences we observed among species.

Cuticle strength of claws—assumptions

To compute ultimate tensile strength of cuticle based on failure of intact claws, we were obliged to make several simplifying assumptions. The indirect method we used, based on linearly elastic theory applied to cantilevered beams (Young, 1989), assumes (I) that the pollex, or fixed finger, of the claw exhibited a constant cross-section along its length; (II) that the cuticle is isotropic and homogeneous; (III) that shape variation along the length of the pollex, such as caused by teeth, does not create local points of stress concentration; and (IV) that tensile strength was less than compressive strength (*i.e.*, that the cuticle failed in tension).

The taper of the pollex (violation of assumption I) undoubtedly introduced some error; however, Young (1989, p. 181) notes that tapers of 30°–40°, similar to those observed in the pollex of *Cancer* claws, would cause extreme fiber stress to be overestimated by only 5%–10%, so although our estimates of tensile strength may be somewhat high, this overestimate should be less than 10%.

Crustacean cuticle is undoubtedly neither isotropic nor homogeneous (violation of assumption II), because of its composite structure (Wainwright *et al.*, 1976). In addition, the stronger tanned material found at the tips of the fingers of many brachyuran crab claws (Melnick *et al.*, 1996) is limited to the outer layer of the cuticle in *Cancer* crabs (G. M. Taylor, unpubl. obs.). Unfortunately, we cannot assess how these attributes influenced our estimates. This assumption, however, also applies to estimates of cuticle strength that others have made on the basis of excised pieces of cuticle (Wainwright *et al.*, 1976; Melnick *et al.*, 1996).

Rather surprisingly, cracks did not appear to start preferentially at the base of adjacent teeth where stress might be expected to be concentrated (violation of assumption III); for example, for 22 of the 136 breaks we observed, cracks started at a point between the tip and base of a tooth, rather than at the top (where wear would have been greatest) or the base of a tooth (where fatigue might have been highest). In addition, breaking force exhibited no apparent predictable variation along the length of the pollex, other than to increase towards the tip (Fig. 2a).

Finally, we were confident that the pollex failed in tension on the upper surface (assumption IV) because all but five of 141 claw tips fractured cleanly in one piece, indicating failure in tension of the upper margin, rather than buckling of the lower margin as observed in crab walking legs (Hahn and LaBarbera, 1993). Therefore, in spite of the
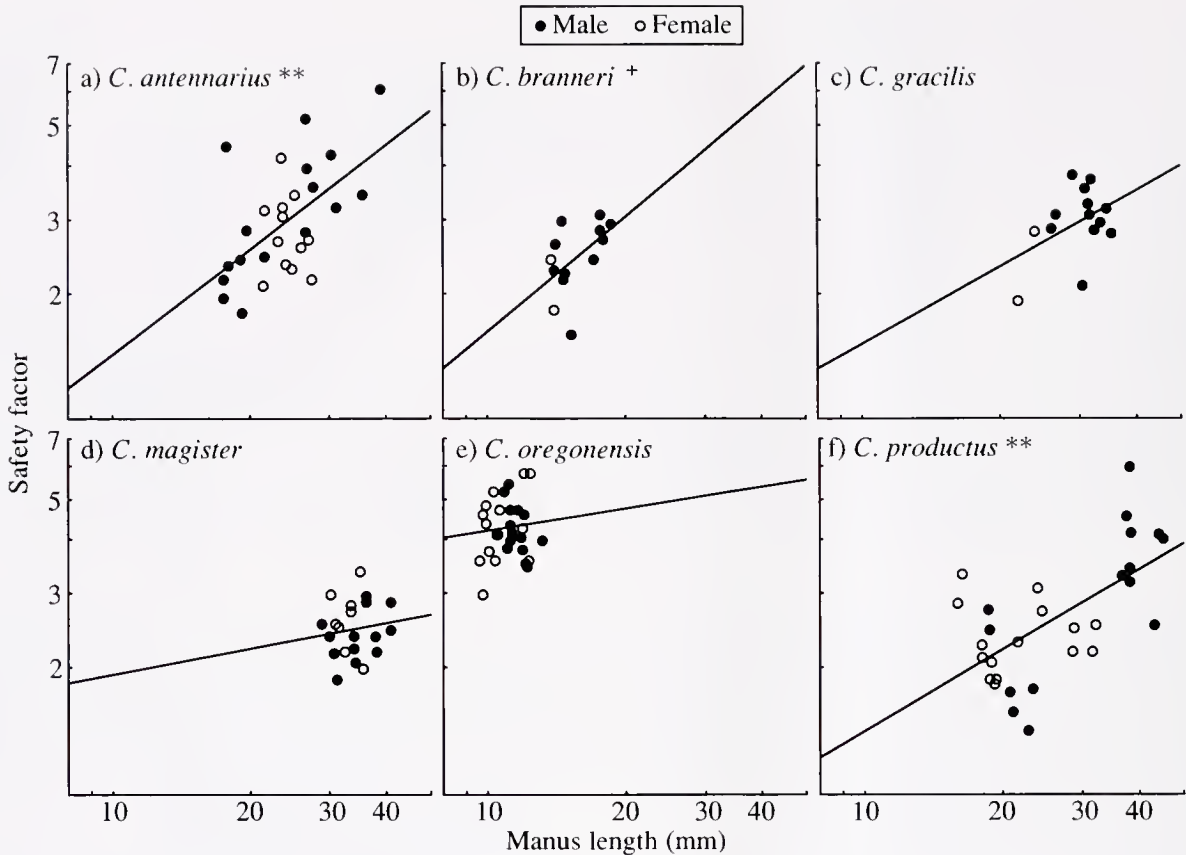
Figure 4. Size-dependence of claw safety factors [breaking force (N)/extreme-maximum biting force (N)] for six species of *Cancer* crabs. Each point represents an individual claw. Lines indicate least-squares linear regressions [see Table IVa for regression statistics and Table Vc for ANCOVA results; $+P < 0.07$, $**P < 0.005$]. Note that both axes are on a logarithmic scale.

potential errors introduced by estimating material properties from the behavior of a complex, intact structure, we believe our estimates are biologically realistic.

Safety-factor allometry

Pollex safety factors increased with increasing claw size for all six *Cancer* species, regardless of whether manus length (Fig. 4, Table IVa) or claw wet weight (Table IVb) was used as the measure of claw size. This increase was highly significant statistically for the two species for which the range of sizes was the largest ($P \leq 0.002$; *C. antennarius* and *C. productus*), and nearly significant for a third species ($P \leq 0.072$; *C. branneri*) (Table IV). Although the intercepts differed among species (see below), the slopes did not differ significantly (Table Vc,d), so we were justified in computing a common slope (*i.e.*, coefficient of allometry) by ANCOVA.

When all six species of *Cancer* crabs were analyzed simultaneously by ANCOVA, claw safety factors increased $\propto$ manus length$^{0.65 \pm 0.094}$ (mean $\pm$ SE) or $\propto$ claw wet

weight$^{0.22 \pm 0.030}$ (Fig. 4, Table Vc,d). Viewed another way, the allometric coefficients for maximum biting force were significantly less than for breaking force. Maximum biting force increased $\propto$ manus length$^{1.49 \pm 0.082}$ (Table Vf), while breaking force increased $\propto$ manus length$^{2.13 \pm 0.0814}$ (Table Vg), yielding a difference in the coefficients of 0.64 ($= 2.13 - 1.49$). Therefore, regardless of how they were computed, safety factors increased approximately $\propto$ manus length$^{0.6}$. If breaking force and biting force varied isometrically, then the scaling coefficient for safety factors (a ratio of the two) should have been zero, so the observed coefficient was significantly greater than expected for isometry. Size-adjusted safety factors also differed among species (Taylor *et al.*, in press).

Both relatively thicker cuticle and relatively weaker biting forces contributed to the higher safety factors of larger *Cancer* claws. When all six species were analyzed together, lateral cuticle thickness of the pollex (dimensions *h* and *i*, Fig. 1) increased $\propto$ manus length$^{1.31 \pm 0.078}$ (Table Vh), so cuticle cross-sectional area would increase $\propto$ manus

Table IV

Size-dependence of pollex safety-factors for claws from six species of Cancer *crabs*

Species	n	Slope (SE)	Intercept (SE)	P	r
a) log(safety factor) (Y) *vs.* log(manus length, mm) (X)					
1. *C. antennarius*	28	0.827 (0.2393)	−0.673 (0.0215)	0.002	0.561
2. *C. branneri*	13	0.900 (0.4513)	−0.692 (0.0230)	0.072	0.515
3. *C. gracilis*	14	0.609 (0.3645)	−0.430 (0.0228)	0.121	0.434
4. *C. magister*	21	0.203 (0.3507)	0.079 (0.0153)	0.570	0.132
5. *C. oregonensis*	30	0.178 (0.3646)	0.446 (0.0138)	0.630	0.092
6. *C. productus*	30	0.633 (0.1520)	−0.483 (0.0223)	<0.001	0.618
b) log(safety factor) (Y) *vs.* log(claw wet wt., g) (X)					
1. *C. antennarius*	28	0.247 (0.0734)	0.269 (0.0218)	0.002	0.551
2. *C. branneri*	13	0.307 (0.1514)	0.328 (0.0230)	0.067	0.522
3. *C. gracilis*	14	0.211 (0.1400)	0.282 (0.0233)	0.157	0.399
4. *C. magister*	21	0.103 (0.1175)	0.292 (0.0150)	0.392	0.197
5. *C. oregonensis*	30	0.060 (0.1138)	0.633 (0.0138)	0.599	0.100
6. *C. productus*	30	0.216 (0.0485)	0.256 (0.0218)	<0.001	0.645

Least-squares linear regression equations; slopes correspond to coefficients of allometry. Safety factor = ratio of breaking force/maximum bite force; isometry for safety factors should be 0 (see text). SE = standard error; r = correlation coefficient.

length$^{2.6}$. Since breaking force should scale ∝cross-sectional area for linearly elastic structures loaded in bending and of constant material properties and shape (see Eq. 1 in Methods), this coefficient significantly exceeded that for breaking force (∝manus length$^{2.13}$; $P < 0.001$). Furthermore, because of the longer time between molts, the cuticle of larger claws in our samples would likely have accumulated more stress cracks and wear than smaller ones, so the

Table V

Overall size-dependence of mechanical and morphological attributes of Cancer *crab claws*

Slope$_{comm}$ (SE)	Range (n_s)*	r^2_{comm}	P	P_{sp}
a) log(ultimate stress, MN m^{-2}) (Y) *vs.* standardized pollex position (X)				
0.30 (0.059)	0.43–0.62 (2)	0.32	<0.001	0.20
0.21 (0.055)†	(none significant)	0.11	<0.001	0.98
b) log(ultimate stress, MN m^{-2}) (Y) *vs.* log(manus length, mm) (X)				
−0.75 (0.144)	−0.81−−0.62 (2)	0.32	<0.001	0.96
−0.62 (0.135)†	−0.64−−0.58 (2)	0.35	<0.001	0.97
c) log(safety factor) (Y) *vs.* log(manus length, mm) (X)				
0.65 (0.094)	0.63–0.83 (2)	0.58	<0.001	0.72
d) log(safety factor) (Y) *vs.* log(claw wet wt., g) (X)				
0.22 (0.030)	0.22–0.25 (2)	0.59	<0.001	0.83
e) log(median-maximum biting force, n) (Y) *vs.* log(manus length, mm) (X)				
1.52 (0.072)	0.95–2.21 (6)	0.90	<0.001	0.045
f) log(extreme-maximum biting force, n) (Y) *vs.* log(manus length, mm) (X)				
1.49 (0.082)	0.93–2.36 (6)	0.88	<0.001	0.081
g) log(breaking force, n) (Y) *vs.* log(manus length, mm) (X)				
2.13 (0.081)	1.54–2.54 (5)	0.88	<0.001	0.35
h) log(lateral cuticle thickness of pollex‡, mm) (Y) *vs.* log(manus length, mm) (X)				
1.31 (0.078)	1.20–1.92 (5)	0.76	<0.001	<0.001

$n = 136$ claws (usually two per crab) for all analyses except a and b, for which $n = 125$. Safety factor = ratio of breaking force/maximum bite force. Slope$_{comm}$ = common slope from a one-factor ANCOVA (species was the grouping factor); expected slopes for isometry relative to manus length are 1.0 for ultimate stress (b), 0.0 for safety factors (c, d), 2.0 for biting force (e, f), 2.0 for breaking force (g), and 1.0 for cuticle thickness (see text). SE = standard error. n_s = number of statistically significant slopes for individual *Cancer* species out of six. r^2_{comm} = coefficient of determination for common slope from ANCOVA. P = probability that the common slope did not differ from zero. P_{sp} = probability that slopes did not differ among species.

* Range of slopes among species exhibiting a significant slope.

† The same ANCOVA design but conducted on residuals obtained separately for each species from the regressions in Table II.

‡ Average of dimensions h and i in Fig. 1. See Tables II, III and IV for regression statistics for individual species.

observed coefficient of 2.13 probably underestimates that for pristine claws. Therefore, the allometric increase in cuticle thickness alone would be sufficient to yield a significant positive allometry for safety factors in pristine claws, even if relative biting force did not decline with increasing size; we would thus expect an even higher positive allometry than the 0.6 actually observed had we been able to use pristine claws.

The lower-than-expected scaling coefficient for maximum biting force was not an artifact of size-dependence in our measurement protocol, because (a) the gape angle at which biting force was measured was kept constant for all claw sizes, (b) the location of the load wire scaled isometrically ($\propto$ manus length$^{0.96 \pm 0.025}$) (data not shown), (c) the transducers were recalibrated before and after each set of measurements, and (d) the scaling coefficients did not differ among species, even though average claw length differed among species by more than threefold. Nor was it due to size-dependent changes in mechanical advantage. In all but one species, mechanical advantage did not vary significantly with size. In *C. productus*, mechanical advantage actually increased with increasing size, so the lower-than-expected coefficient of allometry for maximum biting force was even more puzzling.

Potential limitations due to small sample sizes and narrow size ranges

Coefficients of allometry based on small sample sizes or narrow size ranges can be misleading because of statistical uncertainties (LaBarbera, 1989). For only two species we studied did the size range approach or exceed a factor of two (*C. antennarius* and *C. productus*) and, perhaps unsurprisingly, we most commonly obtained statistically significant associations with claw size for these two species (Tables II and IV). We may thus be premature in concluding that safety factors increase allometrically, and in the same fashion, in all six *Cancer* species.

In spite of small sample sizes and size ranges for four species (Table IV), coefficients of allometry for safety factors were nonetheless positive for all six species, and the slope was nearly significant for one of the remaining species ($P \leq 0.072$, *C. branneri*). In addition, we could not reject the hypothesis that the slopes were statistically indistinguishable using ANCOVA (Table Vc,d), even for the species for which we had reasonable size ranges. Therefore, with the present data we are obliged to accept the simpler hypothesis that safety factors increase similarly with increasing claw size for all six *Cancer* species.

Discussion

Cuticle strength in Cancer crab claws

In spite of the functional significance of claws (Warner, 1977; Brown *et al.*, 1979; Seed and Hughes, 1995) and the

impact that claw failure has on feeding ability (Juanes and Hartwick, 1990; Juanes and Smith, 1995), little is known about their mechanical properties other than biting force or mechanical advantage (Warner and Jones, 1976; Elner, 1978; Elner and Campbell, 1981; Blundon, 1988; Kaiser *et al.*, 1990; Levinton and Judge, 1993; Levinton *et al.*, 1995; Preston *et al.*, 1996). In addition, we are aware of only three reports of tensile strength in crustacean cuticle, and only one was for claw cuticle. The tensile strength of carapace cuticle reported for two portunid crabs is approximately 30 MN m^{-2} [Wainwright *et al.* (1976, Table 5.3) for *Carcinus maenas*, and Hepburn *et al.* (1975) for *Scylla serrata*], and Melnick *et al.* (1996) report fracture strength in three-point bending of 109 MN m^{-2} in the black cuticle of the claw tips and 32 MN m^{-2} ($n = 10$) in the lighter-colored cuticle of the manus in the stone crab (*Menippe mercenaria*). Although we computed stress on intact claws, as opposed to excised pieces of cuticle loaded in three-point bending, our estimates of breaking strength in *Cancer* claws (40–120 MN m^{-2}) nonetheless agree quite well with those of Melnick *et al.* (1996), in spite of the simplifying assumptions we were obliged to make (see *Cuticle strength of claws—assumptions* in the Results).

Our results (Fig. 2b, Table IIa) also support the conclusion of Melnick *et al.* (1996) that the distal cuticle on the fingers of brachyuran claws, often black in color, is a stronger material than other claw cuticle. This stronger material towards the claw tip ensures that the force at which the pollex breaks remains roughly constant along its length (Fig. 2a), even though the cross-sectional area declines distally. It may also increase the abrasion resistance of the claw tip, since crabs forced to feed for extended times on hard-shelled prey often exhibit severe wear of the teeth and tip of both the dactyl and pollex (A. R. Palmer, unpubl. obs.). Material properties of the claw cuticle therefore appear finely tuned to the mechanical demands placed upon it.

Within- and among-species variation in cuticle strength

Unlike previous studies of cuticular properties, our experiments were designed to assess cuticle-strength variation as a function of claw size, both within and among closely related crab species. Somewhat surprisingly, cuticle strength decreased with increasing claw size both within and among the six *Cancer* species we examined (Fig. 3).

Two observations suggest that this decline may reflect increased wear and fatigue that larger claws experienced before we measured breaking strengths. First, the intermolt interval increases with increasing size in *Cancer* crabs (Orensanz and Gallucci, 1988) and although we attempted to use crabs in mid-intermolt throughout, larger crabs may have been further away from their most recent molt and their claws may thus have experienced more wear or fatigue. Second, *C. oregonensis*, whose claws exhibited gen-

erally lower cuticle strength for a given claw size (Fig. 3), matures at a considerably smaller body size (<25 mm carapace width) than the other *Cancer* species we studied (generally >60 mm carapace width; Orensanz and Gallucci, 1988). Here again, because intermolt intervals are longer for older crabs, claws of *C. oregonensis* may have accumulated more wear or fatigue before we measured their breaking strength than did similar-sized claws in presumably younger individuals of the other species. Regardless of the cause of this relationship, conclusions about differences in cuticle strength among species must take into account the effect of claw size.

Indeed, after controlling for the effects of claw size, cuticle strength varied by up to 100% among the six *Cancer* species we examined (Table III). Even though potentially confounded by differences in cuticle thickness (see *Cuticle strength of claws—patterns* in the Results), these interspecific differences in size-adjusted cuticle strength correlated significantly with interspecific differences in size-adjusted safety factors (Taylor *et al.*, in press): species with weaker cuticle had higher safety factors ($n = 6$, $r = 0.92$, $P = 0.008$ when standardized by manus length, and $r = 0.82$, $P = 0.045$ when standardized by claw weight). Therefore, differences in safety factors among species appear to have evolved at least in part in response to differences in mechanical properties of their cuticle.

Allometry of skeletal safety factors in crab claws

The higher safety factors we observed in larger claws of all six *Cancer* species were consistent with theoretical predictions. Larger claws were expected to have larger safety factors because (a) unpredictability of claw strength should increase in larger crabs due to the longer time to accumulate stress cracks and wear between molts, (b) the costs of lost or damaged claws (Juanes and Smith, 1995) will be more prolonged or severe for larger crabs, and (c) larger crabs probably experience a greater range of extreme forces because the claws are used increasingly for aggression (Juanes and Smith, 1995). Thus this size-dependence appears adaptive.

But why does maximum muscle stress, which has the biggest impact on the size-dependence of safety factors, decline with increasing claw size? Similar declines with increasing claw size in stone crabs (Blundon, 1988), male fiddler crabs (Levinton and Judge, 1993), and lobsters (Elner and Campbell, 1981) suggest a general pattern that remains a significant unsolved phenomenon in claw mechanics and evolution. Perhaps larger crabs actively restrain the maximum stress they generate to avoid damaging their claws. Alternatively, larger claws may generate lower stresses because of some as-yet-unidentified physiological constraints. The former would support our interpretation

that higher safety factors in larger claws are adaptive, whereas the latter would not.

The scaling relation between maximum force and a linear claw dimension might possibly be influenced by the bipinnate arrangement of muscles in crustacean limbs (Warner and Jones, 1976), but we believe this is unlikely. In bipinnate muscles, twice as many muscle fibers attach per unit area of apodeme (the crustacean tendon) because they attach on both sides. Bipinnate muscles therefore generate more force per unit volume than do linear muscles (Goldspink, 1977). In addition, muscle fibers attach to the apodeme at an angle, so their per-fiber contribution to the final biting force is less than in typical vertebrate skeletal muscle, where fibers lie roughly parallel to the tendon (Goldspink, 1977). Nonetheless, these two factors affect only the force produced *per unit area of apodeme*. They do not affect the expected allometric relation between maximum force and claw length unless they too vary allometrically. Maximum biting force should therefore still increase $\propto$apodeme area (*i.e.*, $\propto$claw length$^{2.0}$) for bipinnate muscles, just as it should for linear muscles.

The higher safety factors we observed in larger claws did not appear to affect the probability of failure in the field. Among the six *Cancer* species we examined, 9.2% of crabs had injured claws and 28.9% were missing or regenerating one or both claws ($n = 671$). As injuries leading to death would have been under-represented, actual injury rates were probably higher. Significantly, in the two species for which we had adequate sample sizes, the incidence of neither regenerating nor injured claws varied significantly with claw size: $P = 0.44$ and 0.94 respectively for *C. productus* ($n = 285$ crabs: one or both claws missing or regenerating $= 33.0\%$, or injured $= 8.4\%$) and *C. gracilis* ($n = 99$ crabs: one or both claws missing or regenerating $= 41.4\%$, or injured $= 17.2\%$) (Taylor *et al.*, in press). However, because larger claws should accumulate more wear during their longer intermolt intervals and thus be more likely to fail, their higher safety factors nonetheless appear to have reduced the probability of failure to levels similar to those of smaller crabs.

Allometry of skeletal safety factors in other taxa

In other taxa, safety factors vary in many ways with increasing body size or age. As body size or age increases within species, safety factors may either increase, decrease, or exhibit a U-shaped pattern (Table VIa). Within many mollusc species, shell weight or thickness increases disproportionately with increasing body size (Currey, 1977; Palmer, 1981, 1992), suggesting that safety factors also increase with body size (Preston *et al.*, 1996) since the sizes of shell-breaking predators, and hence potential load distribution, should remain about the same. Only for bovid horns

Table VI

Dependence of safety factors on size or age in various taxa and structures

| Taxon and trait | Safety factor | | | Reference |
	Load type		Dependence*	
a) Intraspecific variation				
Human female long bones	locomotion	A	decrease†	Biewener (1993)
Bovid horns	fighting	S/A	none‡	Kitchener (1991)
Spider walking legs	locomotion	S/A	decrease	Prang (1977)
Cockroach walking legs	locomotion	S/A	decrease	Prang (1977)
Crab claws	biting force	S/A	increase§	This study
Mollusc shells	breaking force	S/A	increase¶	Preston *et al.* (1996, see text)
Kelp stipe	wave stress	S	none	Friedland and Denny (1995)
Equisetum stems	self-loading	S	decrease	Niklas (1989)
Shade-intolerant tree trunks	self-loading	S/A	decrease	King (1991)
Early-successional tree trunks	self-loading	S/A	decrease	Claussen and Maycock (1995)
Shade-tolerant tree trunks	self-loading	S/A	U-shaped	King (1991)
Late-successional tree trunks	self-loading	S/A	U-shaped	Claussen and Maycock (1995)
b) Interspecific variation				
Mammalian long bones	locomotion	S	none#	Biewener (1990)
Tree trunks	self-loading	S	none¶	McMahon and Kronauer (1976)
Tree trunks	self-loading	S	none**	Niklas (1994)
Various nonwoody plant stems	self-loading	S	decrease††	Niklas (1994)
Herbaceous plant stems	self-loading	S	decrease§§	Niklas (1995)

* S = explicitly tests for size-dependence; A = explicitly tests for age-dependence; S/A = size- and age-dependence confounded.

† Due to osteoporosis; inferred assuming load distributions were not age-dependent.

‡ True for 8 species.

§ True for 6 species.

¶ True for many species.

Interspecific variation over >3 orders of magnitude of body mass.

** True for 56 species.

†† True for multiple species: mosses ($n = 40$), pteridophytes ($n = 16$), dicot herbs ($n = 120$), palms ($n = 17$).

§§ True for 76 species.

do safety factors appear not to change with increasing body size (Kitchener, 1991).

Rather few extensive studies of interspecific variation have been conducted, but safety factors appear to vary less with size among species of mammals and trees than within species (Table VIb). Only for nonwoody plants and palm trees do safety factors appear to vary substantially with size among species.

These patterns raise an obvious question: to what extent is intraspecific variation in safety factors adaptive? Although the data are too few to draw any generalities with confidence, the patterns in Table VIa suggest that increases in safety factors with increasing size may more commonly reflect adaptive variation (the outcome of selection for genotypes that specifically induce changes in safety factors), whereas decreases in safety factors may signal some form of constraint (nonadaptive variation resulting from peculiarities of the ways in which organisms grow). The evidence for crab claws seems clear: longer intermolt intervals at larger size, increased variability in cuticle strength due to wear and fatigue, and increased cost of failure should all favor higher safety factors (this study). Similarly, for many molluscs and

other organisms whose defensive skeletons permit an *escape in size* (Paine, 1976; Palmer, 1990), larger size results in lower vulnerability; therefore, higher safety factors appear adaptive.

In contrast, safety factors decline with increasing size in the walking legs of insects and arachnids (Prang, 1977) and in the *rind-core* type stems of many nonwoody plants (Niklas, 1989, 1995). Indeed, for both arthropod limbs (Currey, 1967) and rind-core type plant stems (Niklas, 1994), mechanical limits to strength appear to determine the upper limit to body size, which strongly implies that safety factors decline with increasing proximity to a critical size and that this decline is not adaptive. One might also expect the safety factors of long bones in the walking legs of large-bodied vertebrates to decline nonadaptively with increasing body size, because of an unavoidable tradeoff between the mechanically necessary allometric increases in cross-sectional area required to support a greater body mass and the increased cost of producing and transporting heavier skeletal elements (Schmidt-Nielsen, 1984). Similarly, any time the future contribution to fitness declines with increasing size or age, safety factors might decrease nonadaptively, as ob-

served in the long bones of human females (Table VIa; Biewener, 1993).

Two relations in the preceding discussion require additional comment. First, the argument for adaptive size-dependence in the safety factors of molluscan shells is not entirely untainted by potential constraints. In marine gastropods, and probably in many heavily skeletonized marine invertebrates, the maximum rate of body growth at small size may be constrained by the maximum rate of calcification, which in turn may be limited by the physical chemistry of crystal growth (Palmer, 1981). This *calcification-rate constraint* imposes a cruel tradeoff on small individuals: rapid growth is incompatible with increased skeletal defense. So, while the increase in relative shell thickness with increasing size observed in so many molluscs is likely to be adaptive, because it reduces vulnerability to shell-breaking predators, the lower relative shell weight at small size, which is responsible for the observed trend, may be strongly influenced by the calcification-rate constraint. Therefore, perhaps unsurprisingly, not all positive correlations between safety factors and body size may arise for purely adaptive reasons.

Second, whereas declines in safety factors with increasing size may typically signal some kind of constraint, such declines might be adaptive under unusual situations in which controlled failure may enhance fitness. For example, fragmentation of corals may actually promote dispersal and colonization (Highsmith, 1982), but at small size competitive interactions may favor larger colonies (Sebens, 1983). Under these conditions, selection should favor reduced vulnerability to fragmentation at small size but enhanced vulnerability at larger size. Clearly, this type of adaptive decline in safety factors would be limited to colonial organisms.

Acknowledgments

Literature Cited

Alexander, R. M. 1981. Factors of safety in the structure of animals. *Sci. Prog.* 67: 109–130.

Alexander, R. M. 1982. *Optima for Animals.* Arnold, London. 112 pp.

Alexander, R. M. 1983. *Animal Mechanics.* Blackwell, London. 301 pp.

Alexander, R. M. 1997. A theory of mixed chains applied to safety factors in biological systems. *J. Theor. Biol.* 184: 247–252.

Biewener, A. A. 1982. Bone strength in small mammals and bipedal birds: Do safety factors change with body size? *J. Exp. Biol.* 98: 289–301.

Biewener, A. A. 1990. Biomechanics of mammalian terrestrial locomotion. *Science* 250: 1097–1103.

Biewener, A. A. 1993. Safety factors in bone strength. *Calcif. Tissue Int.* 53 (Suppl): S68–S74.

Biewener, A. A., and K. P. Dial. 1995. *In vivo* strain in the humerus of pigeons (*Columba livia*) during flight. *J. Morphol.* 225: 61–75.

Blundon, J. A. 1988. Morphology and muscle stress of chelae of temperate and tropical stone crabs *Menippe mercenaria. J. Zool. (Lond.)* 215: 663–673.

Brandwood, A. 1985. The effects of environment upon shell construction and strength in the rough periwinkle *Littorina rudis* Maton (Mollusca: Gastropoda). *J. Zool. (Lond.)* A206: 551–565.

Brandwood, A., A. S. Jayes, and R. M. Alexander. 1986. Incidence of healed fractures in the skeletons of birds, molluscs and primates. *J. Zool. (Lond.)* 208: 55–62.

Brown, S. C., S. R. Cassuto, and R. W. Loos. 1979. Biomechanics of chelipeds in some decapod crustaceans. *J. Zool. (Lond.)* 188: 143–159.

Buikstra, J. E. 1975. Healed fractures in *Macaca mulatta*: Age, sex, and symmetry. *Folia Primatol.* 23: 140–148.

Claussen, J. W., and C. R. Maycock. 1995. Stem allometry in a north Queensland tropical rainforest. *Biotropica* 27: 421–426.

Currey, J. D. 1967. The failure of exoskeletons and endoskeletons. *J. Morphol.* 123: 1–16.

Currey, J. D. 1977. Problems of scaling in the skeleton. Pp. 153–167 in *Scale Effects in Animal Locomotion.* T. J. Pedley, ed. Academic Press, New York.

Currey, J. D. 1984. *The Mechanical Adaptations of Bone.* Princeton University Press, Princeton. 294 pp.

Elner, R. W. 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia (Berl.)* 36: 333–344.

Elner, R. W., and A. Campbell. 1981. Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapoda: Crustacea). *J. Zool. (Lond.)* 193: 269–286.

Friedland, M. T., and M. W. Denny. 1995. Surviving hydrodynamic forces in a wave-swept environment: Consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). *J. Exp. Mar. Biol. Ecol.* 190: 109–133.

Goldspink, G. 1977. Design of muscles in relation to locomotion. Pp. 1–22 in *Mechanics and Energetics of Animal Locomotion,* R. M. Alexander and G. Goldspink, eds. Chapman and Hall, New York.

Hahn, K., and M. LaBarbera. 1993. Failure of limb segments in the blue crab, *Callinectes sapidus* (Crustacea: Malacostraca). *Comp. Biochem. Physiol.* 105A: 735–739.

Hephurn, H. R., I. Joffe, N. Green, and K. J. Nelson. 1975. Mechanical properties of a crab shell. *Comp. Biochem. Physiol.* 50A: 551–554.

Highsmith, R. C. 1982. Reproduction by fragmentation in corals. *Mar. Ecol. Prog. Ser.* 7: 207–226.

Horst, M. N., and J. A. Freeman. eds. 1993. *The Crustacean Integument. Morphology and Biochemistry.* CRC Press, Ann Arbor, Michigan.

Juanes, F., and E. B. Hartwick. 1990. Prey size selection in Dungeness crabs: The effect of claw damage. *Ecology* 71: 744–758.

Juanes, F., and L. D. S. Smith. 1995. The ecological consequences of limb damage and loss in decapod crustaceans: A review and prospectus. *J. Exp. Mar. Biol. Ecol.* 193: 197–223.

Kaiser, M. J., R. N. Hughes, and D. G. Reid. 1990. Chelal morphometry, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 140: 121–134.

King, D. A. 1991. Tree size. *Natl. Geogr. Res.* 7: 342–351.

Kitchener, A. C. 1991. The evolution and mechanical design of horns and antlers. Pp. 229–253 in *Biomechanics in Evolution,* J. M. V. Rayner and R. J. Wooton, eds. Cambridge University Press, New York.

LaBarbera, M. 1989. Analyzing body size as a factor in ecology and evolution. *Annu. Rev. Ecol. Syst.* **20:** 97–117.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Funct. Ecol.* **7:** 339–345.

Levinton, J. S., M. L. Judge, and J. P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): A result of selection or developmental constraint. *J. Exp. Mar. Biol. Ecol.* **193:** 147–160.

Lowell, R. B. 1985. Selection for increased safety factors of biological structures as environmental unpredictability increases. *Science* **228:** 1009–1011.

Lowell, R. B. 1987. Safety factors of tropical versus temperate limpet shells: Multiple selection pressures on a single structure. *Evolution* **41:** 638–650.

McMahon, T. A., and R. E. Kronauer. 1976. Tree structure: Deducing the principle of mechanical design. *J. Theor. Biol.* **59:** 443–466.

Melnick, C. A., Z. Chen, and J. J. Mecholsky. 1996. Hardness and toughness of exoskeleton material in the stone crab, *Menippe mercenaria*. *J. Mater. Res.* **11:** 2903–2907.

Nations, J. D. 1975. The genus *Cancer* (Crustacea: Brachyura): Systematics, biogeography and fossil record. *Nat. Hist. Mus. Los. Angel. Cty. Sci. Bull.* **23:** 1–104.

Niklas, K. J. 1989. Safety factors in vertical stems: Evidence from *Equisetum hyemale*. *Evolution* **43:** 1625–1636.

Niklas, K. J. 1994. The allometry of safety factors for plant height. *Am. J. Bot.* **81:** 345–351.

Niklas, K. J. 1995. Plant height and the properties of some herbaceous stems. *Ann. Bot.* **75:** 133–142.

Orensanz, J. M., and V. F. Gallucci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of Cancer (Decapoda: Brachyura: Cancridae). *J. Crustac. Biol.* **8:** 187–220.

Paine, R. T. 1976. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57:** 858–873.

Palmer, A. R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature* **292:** 150–152.

Palmer, A. R. 1990. Predator size, prey size, and the scaling of vulnerability: Hatchling gastropods *vs.* barnacles. *Ecology* **71:** 759–775.

Palmer, A. R. 1992. Intraspecific variation in three species of rocky shore gastropods from Hong Kong: correlations among habitats and a comparison with temperate species. Pp. 649–691 in *Proceedings of the Fourth International Marine Biological Workshop. Vol. 1. General Proceedings.*, B. Morton, ed. Hong Kong University Press, Hong Kong.

Prang, H. D. 1977. The scaling and mechanics of arthropod exoskeletons. Pp. 169–181 in *Scale Effects in Animal Locomotion*, T. J. Pedley, ed. Academic Press, New York.

Preston, S. J., I. C. Review, J. F. Orr, and D. Roberts. 1996. A comparison of the strength of gastropod shells with forces generated by crab predators. *J. Zool. (Lond.)* **238:** 181–193.

Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge University Press, New York. 241 pp.

Sebens, K. P. 1983. Size structure and growth rates in population of colonial and solitary invertebrates. *Workshop on Coral Reef Ecology* **1:** 9–15.

Seed, R., and R. N. Hughes. 1995. Criteria for prey-selection in molluscivorous crabs with contrasting claw morphologies. *J. Exp. Mar. Biol. Ecol.* **42:** 25–40.

Smith, L. D., and A. R. Palmer. 1994. Effects of manipulated diet on size and performance of brachyuran crab claws. *Science* **264:** 710–712.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry.* Freeman, New York. 887 pp.

Taylor, G. M., A. R. Palmer, and A. Barton. Variation in safety factors of claws within and among six species of *Cancer* crabs (Decapoda: Brachyura). *Biol. J. Linn. Soc.* (accepted).

Van Valkenburgh, B. 1988. Incidence of tooth breakage among large, predatory mammals. *Am. Nat.* **131:** 291–302.

Van Valkenburgh, B., and F. Hertel. 1993. Tough times at La Brea: Tooth breakage in large carnivores of the late Pleistocene. *Science* **261:** 456–459.

Vermeij, G. J. 1982. Unsuccessful predation and evolution. *Am. Nat.* **120:** 701–720.

Wainwright, S. A., W. D. Biggs, J. D. Currey, and J. M. Gosline. 1976. *Mechanical Design in Organisms.* Arnold, London. 423 pp.

Warner, G. F. 1977. *The Biology of Crabs.* Paul Elek Ltd., London. 202 pp.

Warner, G. F., and A. R. Jones. 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura). *J. Zool. (Lond.)* **180:** 57–68.

Young, W. C. 1989. *Roark's Formulas for Stress and Strain.* McGraw-Hill, New York.